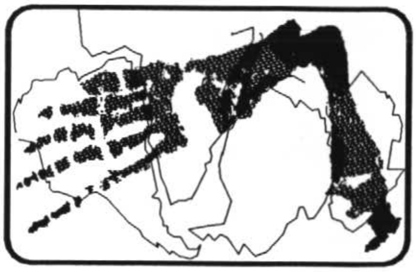


PALEOSCENE #11. Paleobiogeography and plate tectonics

Paul L. Smith
Department of Geological Sciences
University of British Columbia
6339 Stores Road
Vancouver, British Columbia V6T 2B4

Introduction

The bewildering complexity of the modern biosphere is the product of approximately four billion years of evolution. The dissipation of external energy, derived almost entirely from the sun, is the foundation on which the building and maintenance of this complexity rests but there are other important sources of energy whose influence on the history of the biosphere is fundamental. There is mounting, if still somewhat controversial, evidence that the biosphere has been subjected to mass extinctions with a periodicity of 26 million years, perhaps caused by the impact of extra-terrestrial bodies (Alvarez *et al.*, 1980; Raup and Sepkoski, 1982). In a less catastrophic vein, the earth has been continuously dissipating its internal heat which, as the driving force of plate tectonics, has forced the biosphere to adapt to changing plate configurations. Some ecologists believe that ecological systems derive much of their complexity from hierarchies of such independent controls operating at different rates (Allen and Starr, 1982; O'Neill *et al.*, 1986). High levels within a hierarchy operate at relatively slow rates and have an asymmetric relationship with the ecosystem, that is they strongly affect the ecosystem but are unresponsive to changes in the ecosystem itself. This well describes the unrelenting influence of plate motions which, at velocities of a few centimetres per year, generally affect the biosphere over scores or hundreds of millions of years. The species that make up the biosphere on the other hand survive for between one and two million years in the case of rapidly evolving forms such as ammonites, trilobites and graptolites, and 10 to 15 million years in the case of more slowly evolving forms such as bivalves and gastropods (Stanley, 1985).

One of the principle aims of paleobiogeography is to resolve signals in the history of the biosphere that reflect the role of a dynamic paleogeography in guiding the course of evolution. Conversely, the evolution of the biosphere and the tectonic disruption of paleobiogeographic patterns can be used to shed light on the evolution of the lithosphere. The application of biogeographic data to geological problems has a long history. Numerous occurrences of fossil plants and terrestrial vertebrates distributed across South Africa, South America and Australia, for example, implied to nineteenth-century paleontologists that these areas were joined at the time the organisms were alive. It was not fashionable to reassemble the land masses into a supercontinent as shown in Figure 1 because geophysicists of the time argued that the lateral movement of continents was impossible. Consequently, paleontologists and students of modern biogeography were often forced to postulate the existence of land bridges between the continents at various times in the geologic past. It was left to Wegener (1929) to point out that isostasy precluded the disappearance of these convenient land bridges beneath the oceans once they had served their purpose. Leaning heavily on paleobiogeographic evidence, Wegener went on to propose his theory of continental drift which has evolved into the theory of plate tectonics as modern geophysical evidence at first vindicated, and eventually overwhelmed, the original biogeographic evidence.

Until fairly recently most biologists interested in biogeography have placed little emphasis on the role that regional and global geological processes might play in influencing the distribution of organisms. The so-called dispersalist school (*e.g.*, Peake, 1981) certainly looked to the mostly late Tertiary fossil record to provide information on the centres of origin from which newly evolved modern species migrated, but geological features were only considered as potential avenues of migration or as static barriers that organisms struggled to overcome. A land bridge promoting free migration, for example, would be classified as a corridor; a narrow ocean allowing the passage of some shallow marine organisms but not others, would be considered a filter; and a very effective barrier that could only be overcome by chance events such as the rafting of animals on drifting logs across a wide ocean is called a sweepstake route. Dispersal along such migration routes is then chiefly controlled by the adaptive innovations of the organisms and the influence of climate.

Plate tectonics has forced biogeographers to ask new questions because, in the course of geological time, an ocean can be consumed by subduction, a continent split apart by plate divergence, or a mountain chain thrown up by plate collision. Considerations such as these, which are of prime interest to the paleontologist, are now elbowing their way into the biological literature dealing with evolution and biogeography where, in tandem with cladistic analysis, they have given rise to the concept of vicariance biogeography (Nelson and Rosen, 1981). Vicariants are closely related species created when the geographic area inhabited by an ancestor was split by plate tectonics and the resultant sub-populations evolved in separate directions as they became genetically isolated from each other. Evolutionary relationships are established using cladistic analysis, a quantifiable approach based on recognizing shared derived characteristics. It produces a cladogram, a line diagram that illustrates the

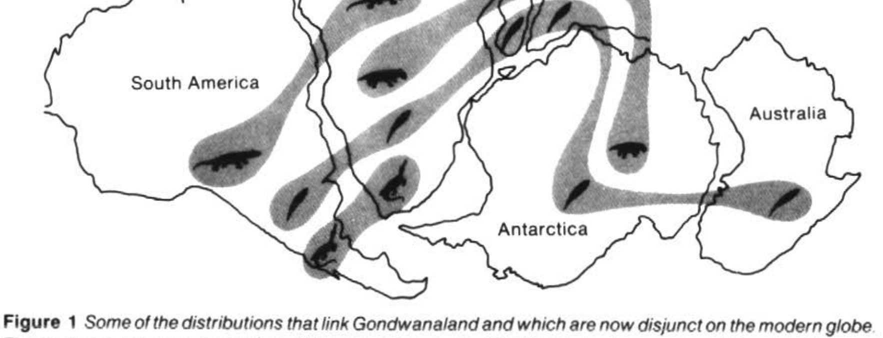


Figure 1 *Some of the distributions that link Gondwanaland and which are now disjunct on the modern globe. The reptile* Mesosaurus *and the plant* Glossopteris *are Permian in age.* Lystrosaurus *and* Cynognathus *are Early Triassic reptiles. (From Colbert, 1973, used with permission).*

hypothesized branching sequence amongst the taxa, which can be compared with the geological area cladogram, that is the splitting sequence of the continents inhabited by the taxa (Nelson and Platnick, 1980). There are of course many biological cladograms that can be constructed for entirely unrelated taxonomic groups, all of which should be congruent with the geological pattern, if indeed vicariance is the controlling factor.

Paleobiogeography then is a broad subject with roots in both biology and geology. This brief review, meant as an introduction to the subject for the geology student, outlines the broad themes of biogeography; considers the sources and methods of analysis of paleobiogeographic data; summarizes the types and combinations of paleobiogeographic patterns that are of geologic significance and presents a selection of case studies.

Biogeographic Patterns

Species consist of populations of interbreeding organisms restricted to specific geographic areas whose limits are a function of biological and environmental factors. Distribution has important evolutionary consequences since widespread species appear to be resistant to extinction and have low speciation rates (Jablonski *et al.*, 1985). Biological limiting factors involve a complex interplay of primary productivity (which may impose endemism at higher levels in the trophic structure), reproductive strategies, mode of life, competition, predation, *etc.*, all of which have changed through time as different organisms evolved or became extinct. Environmental limiting factors include physical barriers and factors linked to climate that change systematically with latitude. Principal among the latter is temperature which directly affects the rates of chemical reactions in which the enzymes controlling life's activities are involved.

Limiting factors commonly affect many species simultaneously, producing patterns of endemism and diversity that permit the definition of biogeographic provinces. Diversity, measured at the specific, generic or family level, depends to some extent on the number of habitats available for exploitation. Continental shelves, for example, may consist of patches of mud, sand and bare rock over which gradients of turbulence and light intensity correlating with water depth are superimposed. In contrast, pelagic environments are much less heterogeneous and their faunas correspondingly less diverse. On a global scale, however, a given environment in tropical latitudes will harbour more species than the same environment at high latitudes (Fischer, 1960; Pianka, 1966). This feature of the biosphere is partly illustrated in Figures 2 and 3 showing diversity decreasing away from the tropics in selected groups of marine and non-marine organisms. Even at the family level, the correlation between diversity and latitude compares well with magnetic data (Figure 3). Diversity gradients symmetrically arranged about the equator have been known since the 18th century when they were recognized by J.R. Forster who explored the southern hemisphere on board Captain Cook's ship, the *Resolution* (Briggs, 1987). The thermal gradient from the equator to the poles, which is believed to be presently at a maximum, correlates well with latitudinal changes in endemism and diversity (Valentine *et al.*, 1978; Jablonski *et al.*, 1985). However, it appears that deep-sea environments, while sparsely populated, have diversity levels almost equal to those of shallow-water tropical environments which led to the idea that the stability of an environment might also be an important regulator of its diversity. (Hessler and Sanders, 1967; Sanders, 1969). The deep-sea might be cold, dark and poorly supplied with food resources but these conditions do not vary and organisms have time to specialize and adapt. Diversity gradients might therefore be a function of the different carrying capacities of low and high latitude environments or of historical factors whereby high latitude environments are less stable. Whatever the causes, we can reasonably expect the diversity of the continental shelf faunas to decrease poleward for any given period in the geological past (*e.g.*, Stehli, 1964, 1968; Addicott, 1970). Although there are several instances where diversity data have been applied to geological problems, some of which are cited in this paper, the potential of this approach has barely been explored.

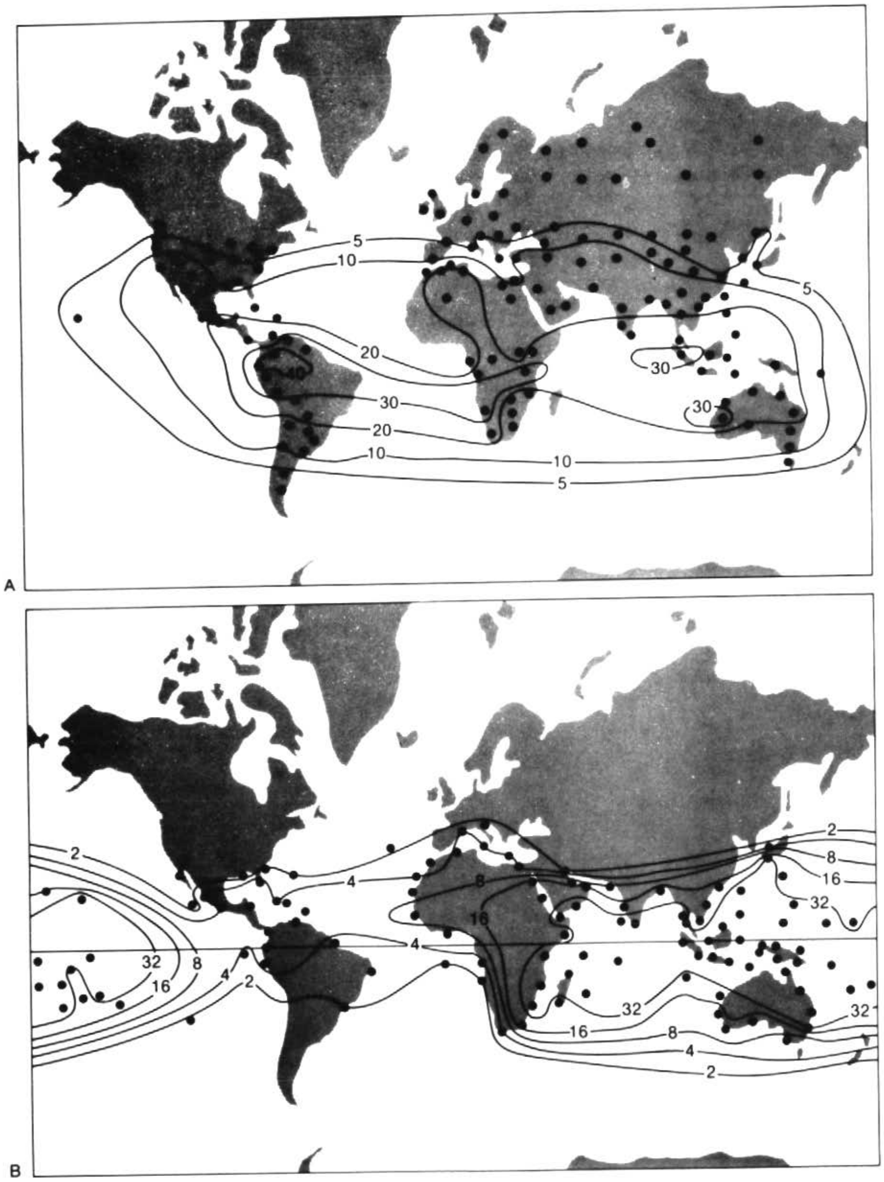


Figure 2 *Examples of modern diversity gradients.* **(A)** *contours showing diversity of lizard genera. Dots represent localities from which data were compiled.* **(B)** *diversity of cypraeid gastropod genera. (From Stehli, 1968, used with permission).*

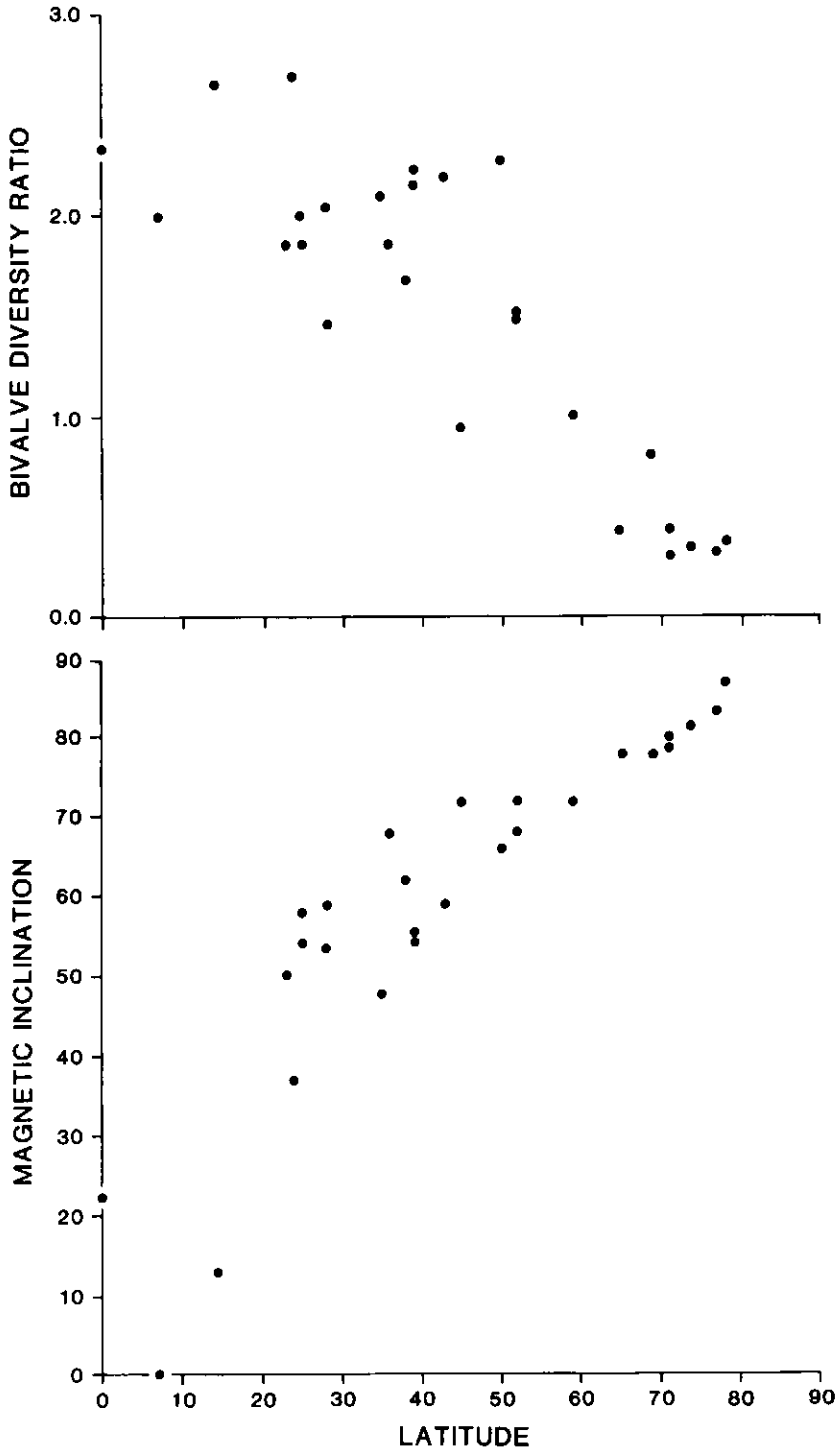


Figure 3 *Latitude dependent data. The two graphs show the magnetic inclination and the bivalve diversity ratio for 27 localities unevenly distributed throughout the northern hemisphere. Magnetic inclination (I) along a meridian should vary as a function of latitude (L) such that tan(I) = 2tan(L). The diversity ratio is defined as (total families-number of cosmopolitan families)/number of cosmopolitan families. (Data from Stehli, 1970; and Vine, 1973).*

On the modern globe deep oceans are amongst the most effective physical barriers to dispersal. Not only are terrestrial faunas living on the continents flanking the deep ocean effectively separated from one another but so are the marine faunas inhabiting the shallow seas of the continental shelves. Provinciality can therefore be viewed as a product of the degree of continental fragmentation and the intensity of the thermal gradient (Valentine *et al.*, 1978).

Paleobiogeographic Data

Most paleobiogeographic data have accrued as by-products of biostratigraphic studies concerned with correlation problems. Establishing the lateral distribution of a taxon is more difficult than establishing its temporal range. Consequently there are no paleobiogeographic equivalents of the compilations by Harland *et al.* (1967) and Sepkoski (1982, 1986) documenting the temporal fossil record. Journals, monographs and the less than comprehensive *Treatise on Invertebrate Paleontology* (Moore and Teichert, 1953-1973) remain the chief sources of paleobiogeographical data, but data quality and availability will undoubtedly improve as groups of specialists build computer databases to collate existing and new information.

There are now numerous paleocontinental and paleogeographical maps that can be used as a base for plotting global biogeographic patterns (Smith and Briden, 1977; Scotese *et al.*, 1979; Barron *et al.*, 1981; Smith *et al.*, 1981; Irving, 1983). The reliability of these maps generally decreases the older the geologic period, becoming conjectural for the Paleozoic. The maps ignore displaced terranes, but terrane maps are becoming avaliable for some parts of the world (*e.g.*, Silberling and Jones, 1984; Howell, 1985).

Paleobiogeography appears to be moving from a descriptive phase to a quantification of patterns that promises a more rigorous understanding of the processes involved in shaping the biosphere. The use of binary coefficients based on presence/absence data is the most common method of gauging similarity (Hazel, 1970). Studies have shown that specific-level biogeographic patterns can also be recognized at the generic and family levels (Simpson, 1980b; Campbell and Valentine, 1977) and, since the probability of collection failure decreases with increased taxonomic rank, this goes some way in alleviating the sampling problems inherent in biogeographic work. It is common experience that both modern and fossil communities contain a few species that are abundant and a comparatively large number that are rare (Krebs, 1978). Binary coefficients ignore this skew and this must be borne in mind whenever interpreting them. It is also important that sampling be as thorough as possible because collection failure causes bias against the less abundant taxa.

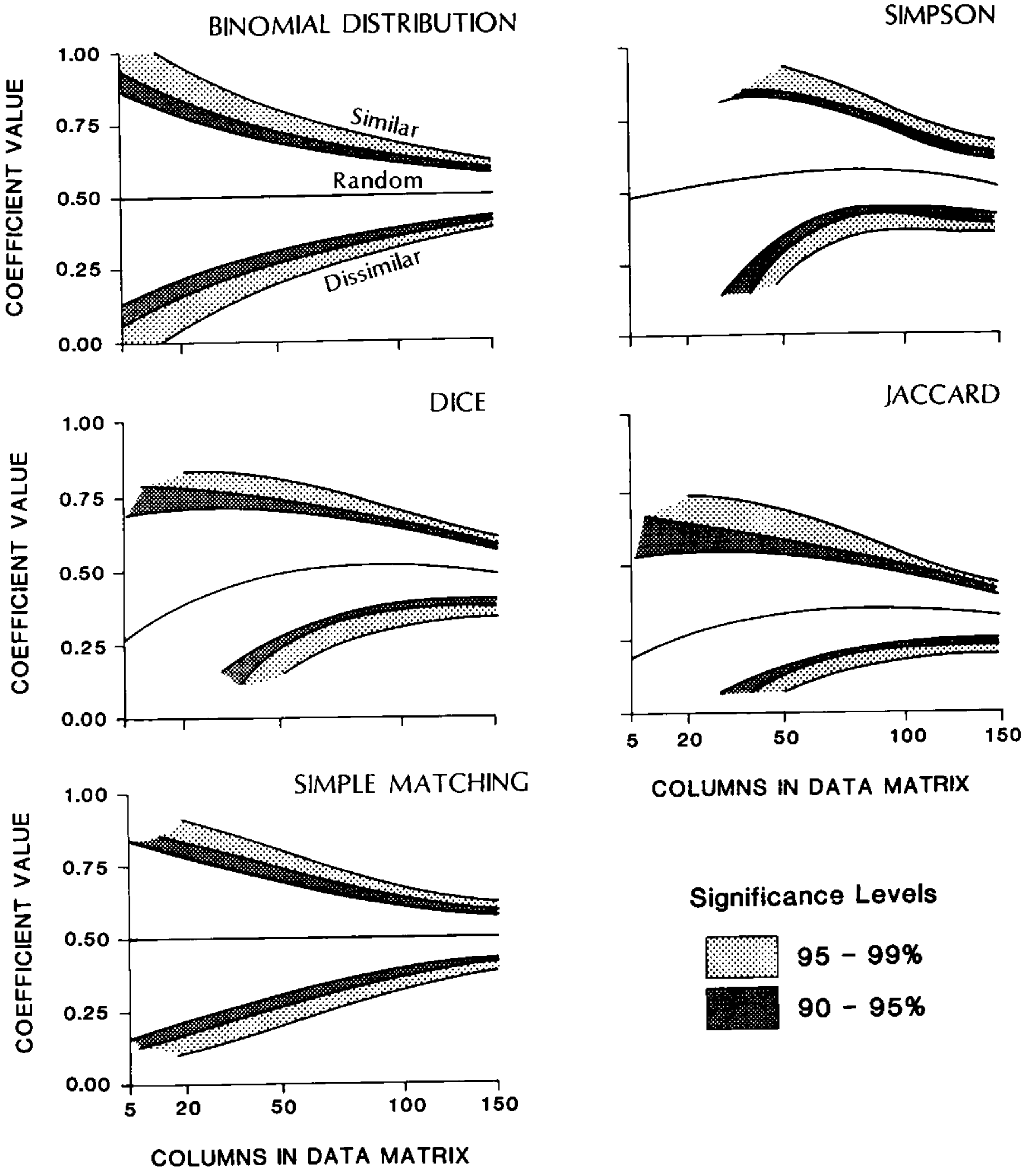


Figure 4 *Monte Carlo simulations for various similarity coefficients compared to an ideal binomial distribution when the number of mutual absences is not greater than 50%. Significance levels may be used to assess the deviation of real data from a random distribution. (From Archer and Maples, 1987).*

Frequently used binary coefficients are the Simpson (Si), Dice (Di), Jaccard (Ja) and Simple Matching (SM) coefficients defined by Archer and Maples (1987) as follows:

$$Si = A/(A+E)$$
$$Di = 2A/(2A+B+C)$$
$$Ja = A/(A+B+C)$$
$$SM = (A+D)/(A+B+C+D)$$

where A = number of taxa common to any 2 samples
B = number of taxa present in sample 1 only
C = number of taxa present in sample 2 only
D = number of taxa which are absent from both samples
E = the smaller value of B or C

In all cases, the coefficient ranges from 0 to 1 (some authors multiply the coefficient by 100) with 0.5 indicating a random distribution, low values indicating dissimilarity and high values similarity.

The coefficients vary in their sensitivity to differences in sample size and in their emphasis on similarity *versus* dissimilarity so that it is common to calculate more than one type of coefficient for each analysis. Until recently, different coefficients could not be compared directly and Raup and Crick (1979) had also criticized their use because it was not possible to derive a statistically meaningful significance level for an analysis. Monte Carlo simulations using random data to calculate the coefficients for different numbers of variables have now generated plots delineating zones of statistical significance when the data set is reasonably dense, *i.e.*, less than 50% absences (Archer and Maples, 1987). In these circumstances, random binary data should have a mean of 0.5 with the spread about the mean becoming less as the number of variables increases. As shown in Figure 4 the simple matching coefficient most closely approximates a binomial distribution; the Simpson and Dice coefficients approximate a binomial distribution when the number of variables is high, but the Jaccard coefficient appears to be unreliable as has been shown empirically by Flessa and Miyazaki (1978). When the data set is sparse (*i.e.*, considerably more than 50% absences), Monte Carlo simulations show that the Dice coefficient best indicates similarity although it cannot be used to make statistically meaningful comparisons of the dissimilarities between samples (Maples and Archer, 1988).

Binary coefficients may be used in cluster analysis to recognize groupings within the distributional data that define biogeographic provinces and reflect environmental discontinuities (Jablonski *et al.*, 1985; *see* Williams, 1973 for an interesting example using Ordovician brachiopods). During the Phanerozoic, the number of marine provinces appears to have varied by an order of magnitude or more (Valentine *et al.*, 1978) which poses its own sampling problems. The recognition of a highly provincialized biosphere requires a greater number of samples distributed over a wider area than for times when provincialism was low (Jablonski *et al.*, 1985). Binary coefficients may also be used in terrane analysis to compare the faunas of allochthonous terranes with provincial patterns already recognized on the stable cratons. The recognition of provincialism and the application in terrane analysis concern either single time planes or narrow intervals of geologic time, but coefficients can also be calculated for successive time intervals to obtain a dynamic picture of paleobiogeographic change.

Paleobiogeographic Patterns

Rearrangement of the lithosphere and the formation of geographic barriers by plate convergence, plate divergence, transform faulting and plate collision may produce two types of biogeographic patterns recognizable in the fossil record (Figure 5): (a) *Disjunct:* patterns of endemism and diversity that are already part of the fossil record may be fragmented and dispersed or brought from distant places and juxtaposed. Correctly piecing together this jig-saw puzzle helps us to understand the configuration of plates and terranes at the time the faunas were fossilized. (b) *Temporal:* patterns of diversity and endemism can be affected directly during the course of time as the

	ENDEMISM	DIVERSITY
DISJUNCT PATTERNS The disruption of fossilized biogeographies	DISJUNCT ENDEMISM Endemic centre fragmentation Biogeographic boundary off-set Tectonic suturing	DISJUNCT DIVERSITY
TEMPORAL PATTERNS The influence of plate tectonics on living biotas	CONVERGENCE DIVERGENCE COMPLIMENTARITY	DIVERSITY AS A FUNCTION OF CONTINENT CONFIGURATION

Figure 5 *Patterns of endemism and diversity caused by the influence of plate tectonics.*

construction and destruction of geographic barriers by plate tectonic processes lead to speciation, competition and extinction. The tectonic plates of group (a) carrying their fossilized cargo have been evocatively described as "Viking Funeral Ships" by McKenna (1973) contrasting with the "Noah's Arks" of group (b) transporting their living communities.

From a geological standpoint, disjunct distributions provide a useful time constraint. The ocean basin or other feature that now separates the disjunct components must have formed after the biogeographic pattern was fossilized. Disjunct distributions also suggest the amount of displacement that has occurred. The types of plate-mediated disruption of endemic patterns that have been recognized in the fossil record are illustrated schematically in Figure 6. An early example of endemic centre fragmentation was recorded by Wegener (1929) who pointed out that the Permian aquatic reptile *Mesosaurus* is only found in southern Brazil and southern Africa. Individuals of the genus *Mesosaurus* were small creatures inhabiting fresh and brackish waters; it does not seem likely that they could have negotiated the broad marine expanse of the South Atlantic other than by some sweepstake method. Wegener preferred the simpler explanation that the South Atlantic was much narrower or perhaps did not even exist during the Permian. Distributions of the Permian and Triassic terrestrial organisms illustrated in Figure 1 are disjunct on the modern globe as a result of the break-up of Gondwanaland.

Tectonic suturing which is the inevitable result of an ocean basin being consumed by subduction and the flanking continental plates ultimately colliding, is illustrated in an example given by Kennedy and Cobban (1976). During the Cretaceous, the Tethyan Ocean was narrowing but its southern shores still supported an ammonite fauna distinct from that on its northern shores (Figure 7). The margins of the Tethyan Ocean can be loosely compared to the blades of a gradually closing pair of scissors with the pivot at the western end of Tethys. At the "pivot" in southern France, Boreal and Tethyan faunas mixed freely and can now be found in the same rock sequences. Passing eastward on the modern globe, however, the gradational transition of the biogeographic boundary is replaced by disjunct communities that have been tectonically juxtaposed within the jumble of plates representing the closure of Tethys. The far eastern portal of the remnants of Tethys closed in the mid-Miocene when New Guinea and Australia, a piece of the then fragmented Gondwanaland, became tectonically sutured to Laurasia in the vicinity of the modern Celebes and Lesser Sunda Islands (Audley-Charles, 1981). This is the site of "Wallace's Line", the biogeographic boundary between the floras and faunas of Asia and Australia.

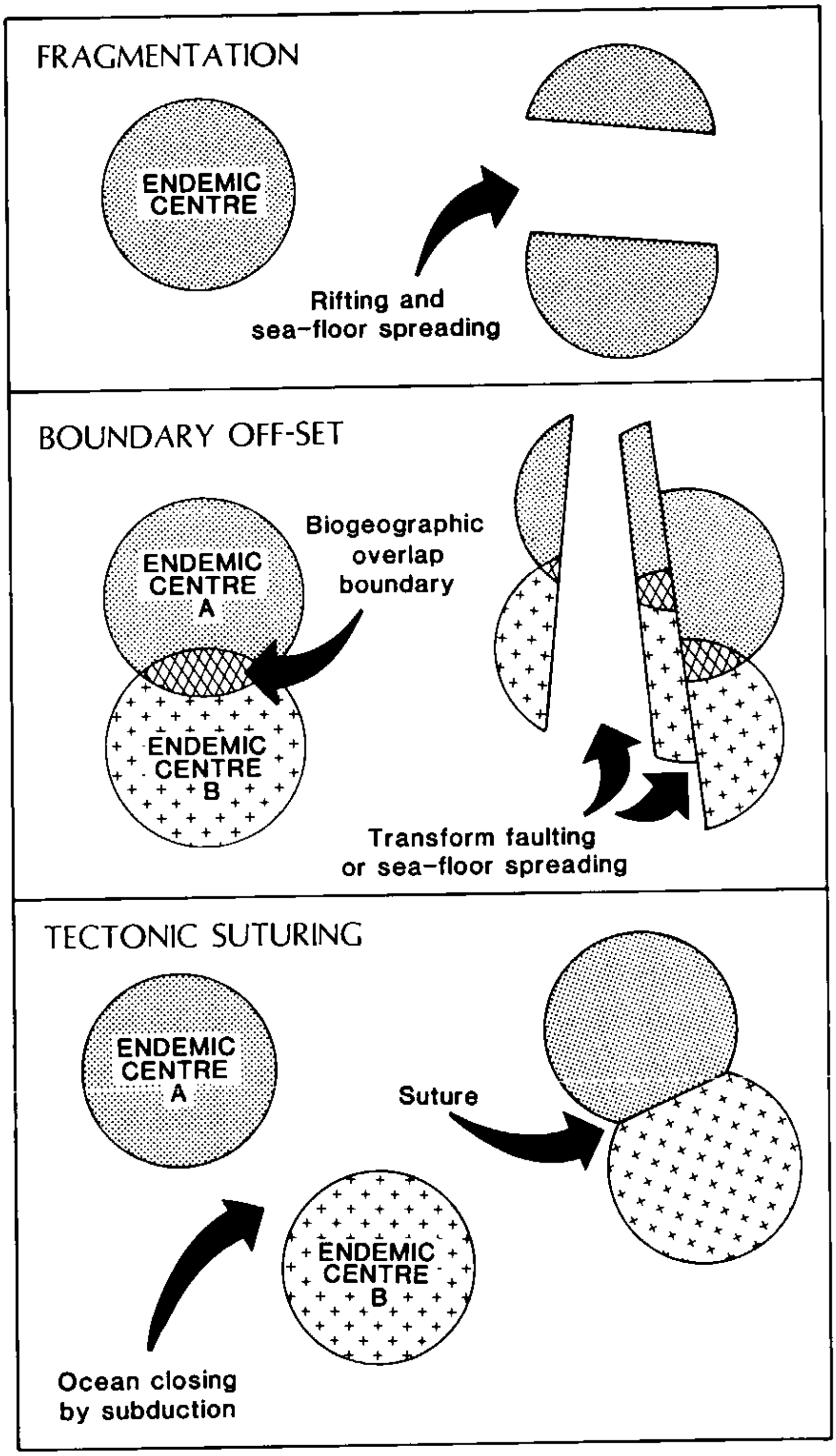


Figure 6 *Disjunct patterns: schematic plan view of plate-mediated rearrangement of fossilized faunal distributions.*

Wallace, who is perhaps best known as the co-discoverer with Darwin of evolution by natural selection, showed remarkable insight in a letter written in January of 1858 to a colleague in London:

> "In the (Malay) Archipelago there are two distinct faunas rigidly circumscribed, which differ as much as those in South America and Africa, and more than those of Europe and North America. Yet there is nothing on the map or on the face of the islands to mark their limits. The boundary line often passes between islands closer than others in the same group. I believe the western part to be a separated portion of continental Asia, the eastern the fragmentary prolongation of a former pacific continent" (George, 1981; Marchant, 1916).

In a paper dealing with the distribution of recent terrestrial mammal faunas, Flessa *et al.* (1979) demonstrated a general feature of endemism by showing a statistically significant, negative correlation between the faunal similarity and the geographic distance between regions. If geographic distance or for that matter the effectiveness of any physical barrier between living communities is altered by plate tectonic activity, this should be reflected in the trend of faunal similarity through time. Hallam (1972, 1973a) has called these temporal trends faunal convergence and faunal divergence for increasing and decreasing similarity, respectively. Some changes in plate configurations lead to a simultaneous faunal convergence and divergence in different parts of the biosphere, a pattern known as complimentarity. An example involving marine and terrestrial faunas can be visualized by considering the course of events subsequent to the situation depicted in Figure 7. During the Oligocene and Miocene, the Tethyan Ocean finally closed, causing the sea to regress from the Middle East and the faunas of the Mediterranean to diverge from those of the Indian Ocean. At the same time, a significant convergence of terrestrial faunas resulted from the cross-migration of mammals between Africa and Eurasia (Hallam, 1973a).

Faunal convergence and divergence are the paleobiogeographic contribution to global diversity, the balance between the extinction and origination of taxa. Kúrten (1969), for example, has pointed to the remarkable contrast in the diversification of reptiles and mammals through time. The so-called age of the reptiles started in the Permian and closed at the end of the Cretaceous when the age of the mammals began. During this 200 million year interval, some 20 major groups of reptiles evolved compared to 30 mammalian groups in the 65 million years since the close of the Cretaceous. At the opening of the age of the reptiles there existed a supercontinent Pangaea consisting of Laurasia to the north and Gondwanaland to the south separated by the Tethys Ocean. As the Mesozoic Era progressed, the supercontinent began to fragment into the modern continents so that by the end of the Cretaceous, marine barriers, perhaps made more effective by eustatically high sea levels, were effectively isolating terrestrial faunas. Each continent began to evolve its own ecologically balanced fauna and global faunal diversity increased. Because the end-Cretaceous mass extinctions so devastated the reptiles it was the mammals that were left to benefit. Some of Kúrten's assumptions are open to question (Charig, 1973), but interestingly Valentine and Moores (1970) showed that shallow-water benthic faunas inhabiting the epicontinental seas also show changes in diversity thought to be a function of continental fragmentation. By plotting the number of well-skeletonized, shallow-water benthonic invertebrate families against time, they illustrated a steady increase in diversity up to the present. Periods of low diversity in the Cambrian and at the end of the Paleozoic correspond to periods of continental amalgamation (Figure 8).

If other factors can be discounted, the influence of plate tectonics on paleobiogeography and evolution should be reflected in the fossil record by various combinations of the patterns tabulated in Figure 5. For example, as an ocean basin forms by rifting and sea-floor spreading it should fragment the fossilized biogeography common to the two separating plates followed by faunal divergence (Figure 9). Conversely, as an ocean

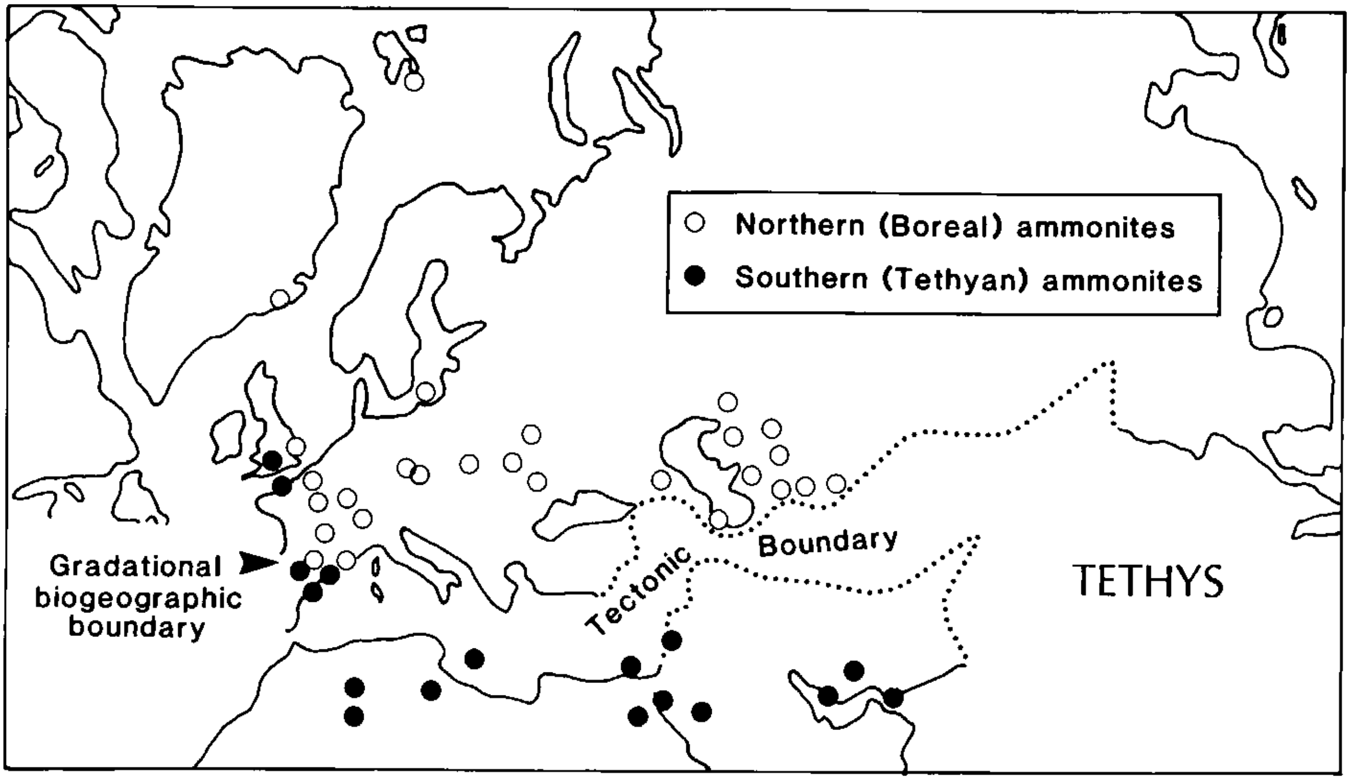


Figure 7 *The distribution of Boreal Hoplitids and "Tethyan" Pseudoceratites during the Albian. For much of the Mesozoic the Iberian Peninsula and southern France were the site of a gradational biogeographic boundary (see also Figure 15b) but to the east the subsequent closure of Tethys brought together endemic faunas in a zone of tectonic discontinuity through the Alpine fold belt and the Zagros thrust complex. (Adapted from Kennedy and Cobban, 1976).*

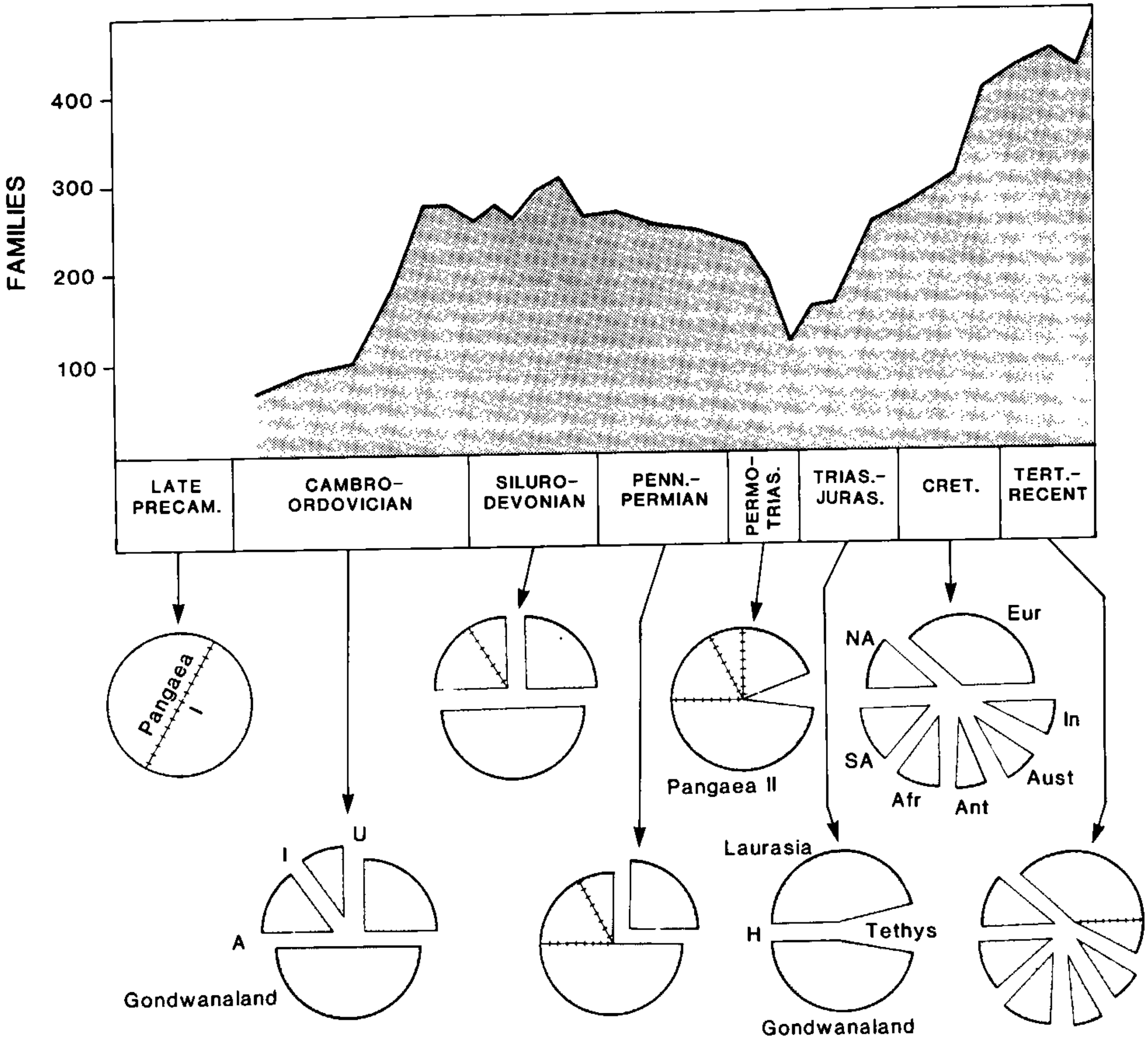


Figure 8 *Family level diversity of well-skeletonized shelf benthos during the Phanerozoic and its relation to plate configurations. (Adapted from Valentine and Moores, 1970, 1972). I, Iapetus ocean (proto-Atlantic); A, pre-Appalachian-Hercynian ocean; U, pre-Uralian ocean; H, Hispanic Corridor.*

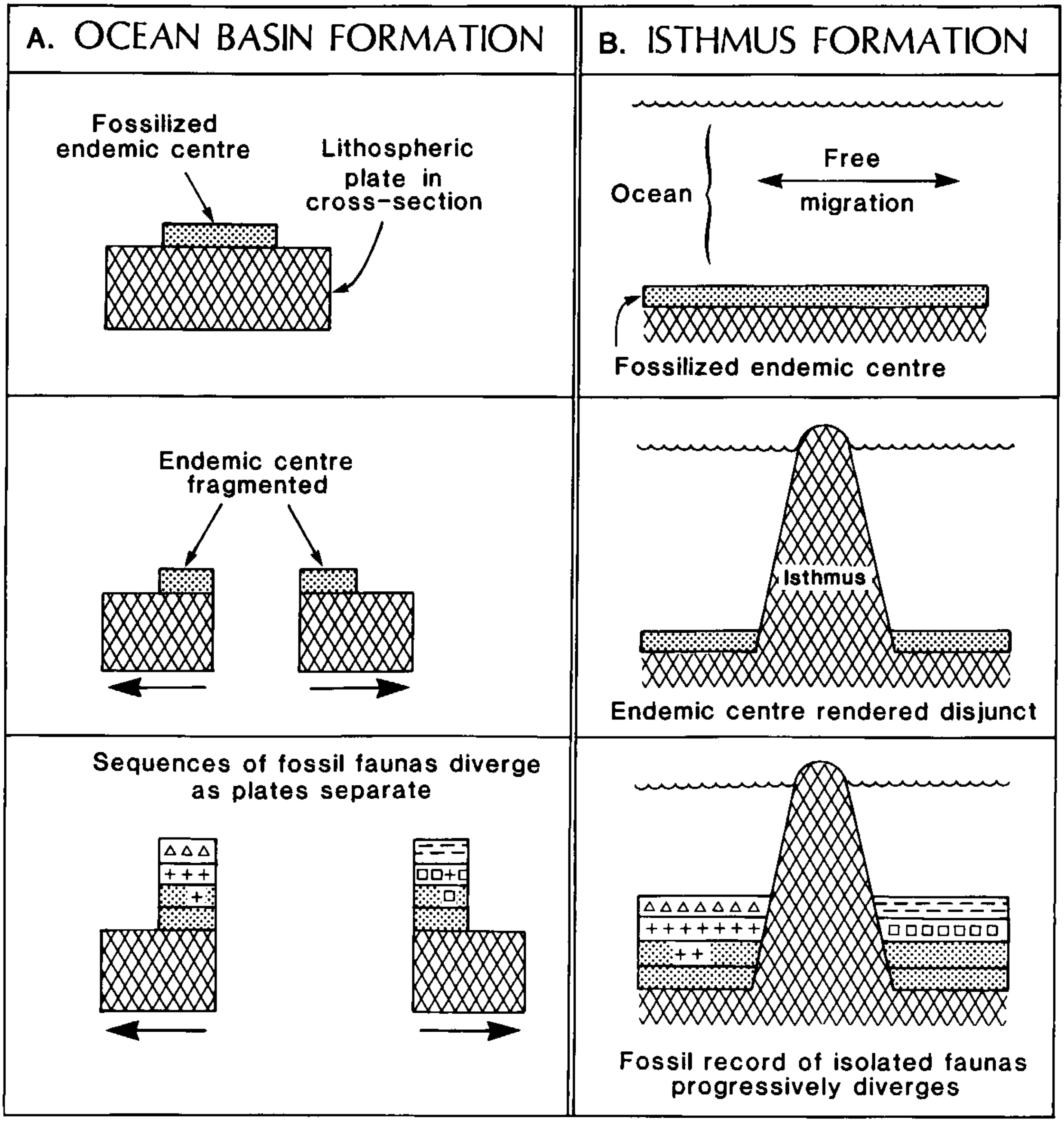


Figure 9 *Temporal patterns: schematic representation of* **(A)** *plate-mediated transport of living biotas causing faunal divergence in the fossil record and* **(B)** *faunal divergence caused by the formation of a physical barrier.*

basin is destroyed by subduction, it should cause faunal convergence between faunas of the physically converging plates followed by tectonic suturing and ultimately a biogeography common to both plates (Figure 10). In practice, the search for various pattern combinations has of necessity been selective in terms of the areas, time periods and taxonomic groups studied. This is evident even in the three better known case histories outlined below which are pieced together from diverse sources.

The Hispanic Corridor and The Panamanian Land Bridge

The similarity coefficients between North and South America for Triassic terrestrial vertebrate families are lower than the coefficients between South America and Eur-Africa suggesting that dispersal between North and South America was already becoming indirect during the early stages of the breakup of Pangaea (Cox, 1974; Briggs, 1987). By the Jurassic, there is convincing geological and biogeographical evidence that a marine connection, called the Hispanic Corridor, had formed sub-parallel to paleolatitude through the present Caribbean and North Atlantic joining the east Pacific with the western end of the ancient Tethys Ocean (Hallam, 1973b; Smith and Tipper, 1986). For example, the dispersal of bivalves along this marine connection is indicated by a plot of the similarity coefficients between Europe and the western Americas for the Early and Middle Jurassic (Hallam, 1983). While the free marine connection between North and South America along the east Pacific is reflected in the constant similarity coefficients, the rising coefficients between the Americas and Europe mark the onset of faunal convergence as at first a few organisms filtered through and finally a busy corridor was in operation by the Middle Jurassic (Figure 11). Early filtering by nascent marine connections between two regions of the biosphere has not been well studied. It is a potential source of information on the differential dispersal abilities of organisms; the equilibrium state of the faunas at either end of the link; and the physical makeup of the link itself. Ship canals that join previously isolated ecosystems are potentially informative analogs except that the time since their construction is short from a geological perspective and their early ecological effects are not well documented (Aron and Smith, 1971). The Suez Canal, for example, was finished in 1869; it is fairly shallow (8-11 m) and has no locks, but it includes the Great Bitter Lake which had salinities of 68 parts per thousand (twice normal marine salinity) when the canal first opened. Relatively recent studies have shown that several phyla have overcome this substantial barrier (some plants and polychaetes in ships' ballast), but the dispersal has been predominantly from the Red Sea to the Mediterranean (127 species south to north, 3 species north to south) suggesting that currents may play an important role (Agur and Safriel, 1981). The subject needs methodical study, but to date there has been no evidence that the Hispanic Corridor was initially open enough to permit the development of a westerly flowing equatorial current. Certainly Westermann and Riccardi (1985) see no asymmetry in the migration of Middle Jurassic ammonites through the Corridor.

As the Hispanic Corridor widened and South and North America separated from each other at a rate in excess of 5 cm per year (Donnelly, 1985), their terrestrial faunas became progressively more isolated. MacArthur and Wilson (1963, 1967) developed an equilibrium model derived from the study of oceanic island biogeography that was subsequently applied at continental scales. The model predicts that the faunal diversity of an isolated area such as an island or continent will attain a dynamic equilibrium that is a function of speciation/immigration rates on one hand and extinction rate on the other.

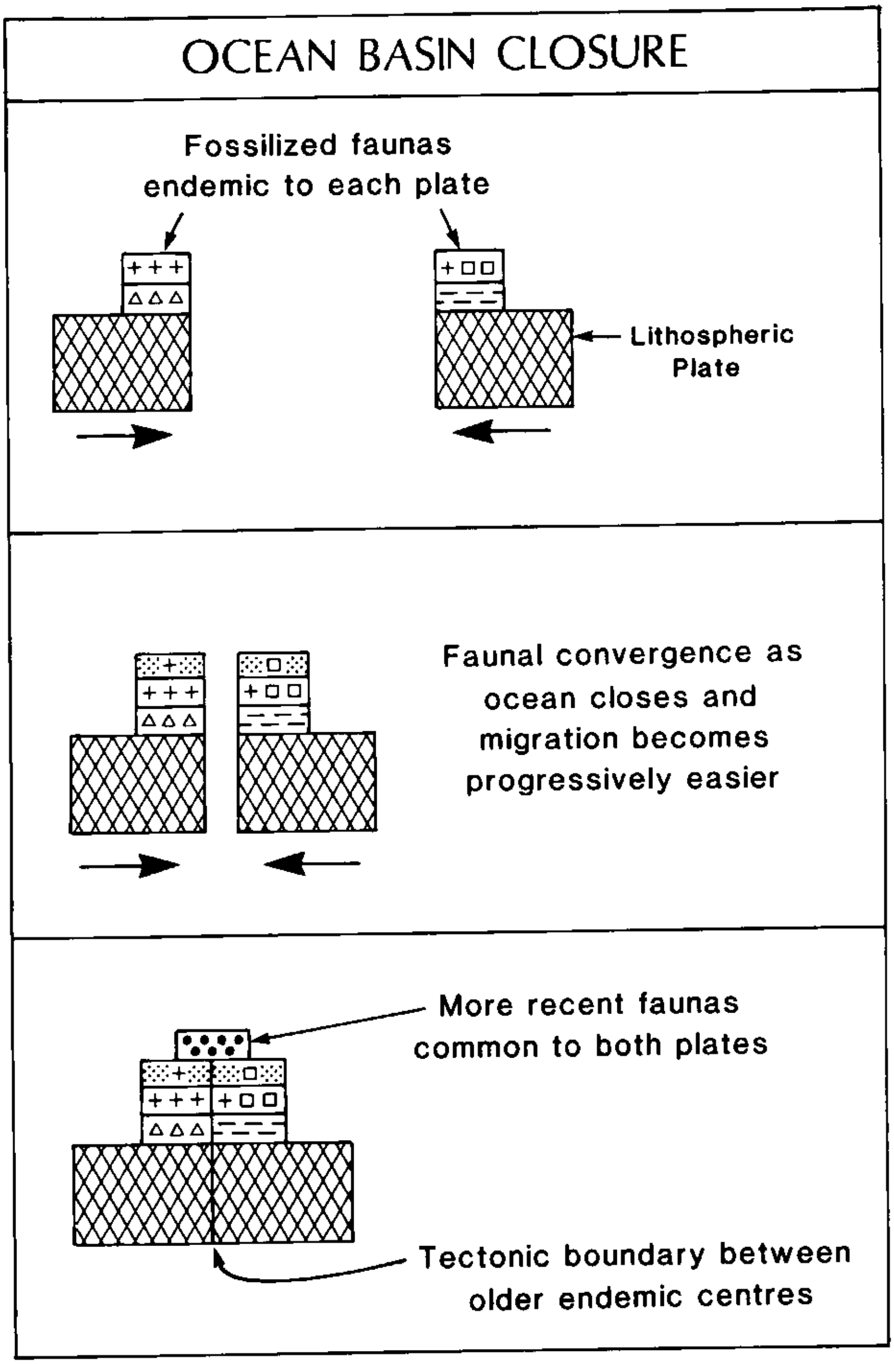


Figure 10 *Temporal patterns: schematic representation of plate-mediated transport of living biotas causing faunal convergence in the fossil record. Dispersal of organisms between plates changes progressively from sweepstake event to free migration as the ocean basin closes*

Larger areas result in higher diversities, lower species turnover rates and longer periods needed to achieve equilibrium. Furthermore, the effect of the source fauna on an isolated fauna receiving immigrants should be proportional to the diversity of the source fauna.

Marshall *et al.* (1982) used the MacArthur-Wilson theory in a study of American land mammals inhabiting savanna grasslands during the Miocene to Pleistocene. Generic-level data show that dynamic equilibrium had been achieved during the long period of Tertiary isolation. South American diversities just prior to land bridge formation remain constant at around 72 per age whereas those of North America, which was not a completely closed system because of periodic immigration from Eurasia *via* the Bering land bridge, are substantially higher and show more variation. The greater generic diversities and generally lower per genus turnover rates for North America (average 0.3 per age *versus* 0.4 for South America) are compatible with equilibrium theory; the area of North America is 24 x 10^6 km^2 compared to South America's 18 x 10^6 km^2 (Marshall *et al.*, 1982).

The breakdown of South America's isolation and the reversal from faunal divergence to faunal convergence with respect to North America began in the late Miocene when the two continents were close enough to permit sweepstake dispersal by island arc hopping. Two genera of ground sloths travelled from south to north and a raccoon genus in the opposite direction (Webb, 1985). The Panamanian land bridge formed during the

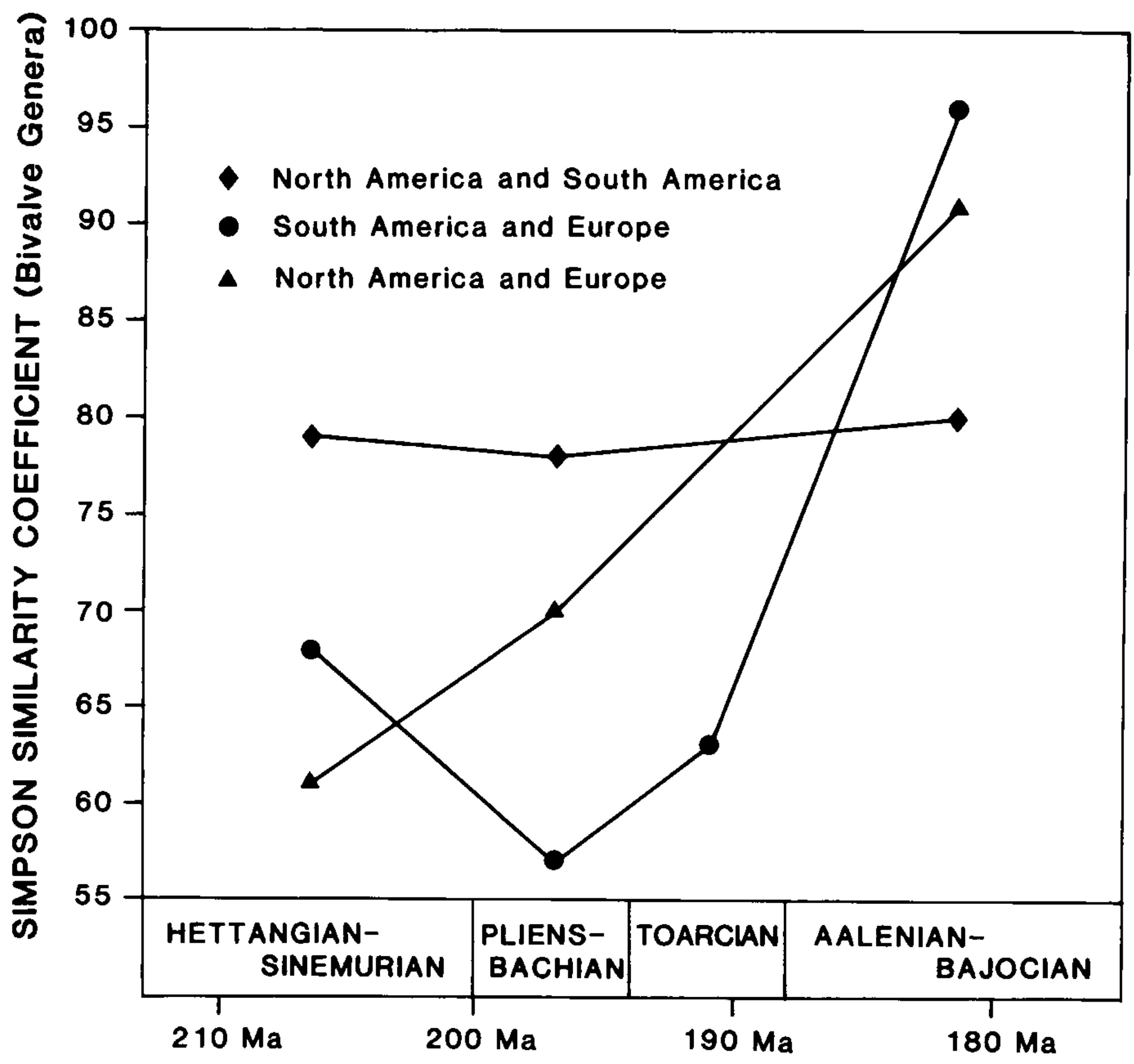


Figure 11 *Faunal convergence — an increase of faunal similarity giving a positive slope to the plot of similarity coefficients against time. Bivalve communities in Europe and the Americas become less endemic as the Hispanic Corridor joining western Tethys and the eastern Pacific opens during the Jurassic. Bivalve data from Hallam (1983); absolute dates from Harland* et al. *(1982).*

Pliocene by a combination of the closure of the Bolivar trough in the region of northwestern Columbia and southern Panama and eustatically lowered sea levels (Marshall *et al.*, 1982; Savin and Douglas, 1985). Complimentarity has been documented at about 3.1 million years when the now separated foraminiferal populations of the Caribbean and the eastern Pacific began to show faunal divergence and also evidence of response to different environmental conditions (Keigwin, 1978).

During the great American interchange as it is sometimes called (Stehli and Webb, 1985), up to 11% of native North American land mammals migrated to South America during any given geological age while up to 7% of South America's genera migrated northward (Marshall *et al.*, 1982). Because of North America's consistently higher diversities, these not significantly different percentages translate into a dominantly north to south traffic. However, the balance of the interchange in proportion to the source faunas and in keeping with equilibrium theory needs to be stressed. What equilibrium theory did not predict was the radically different evolutionary development of the immigrant groups once the interchange had occurred. As shown in Figure 12, the South American genera that reached North America gave rise to relatively few new taxa in marked contrast to the North American genera which radiated rapidly in South America. The interchange of course resulted in an initial diversity jump for both continents, but it was the makeup of the now supersaturated South American biota that changed most drastically as the natives were out-competed and forced to extinction. As a result, approximately 50% of the mammal genera presently living in South America represent, or are derived from, North American invaders (Marshall, 1981).

The Allochthonous Terranes of Western North America

In 1970, Tozer pointed out that the coralline Triassic faunas of the southern Yukon represented warm-water, low latitude faunas that had been displaced north of the cooler water faunas of the same age found in the Peace River area on the craton. This was to be the first of numerous papers documenting the disjunct endemism and diversity of Paleozoic and Mesozoic faunas west of North America's cratonic margin. After the paleobiogeographic anomalies had been first recognized, paleomagnetic evidence was forthcoming and the concept of displaced tectonic terranes evolved (Irving and Yole, 1972; Hillhouse, 1977; Jones *et al.*, 1977; Irving *et al.*, 1980; Monger and Irving, 1980; Coney *et al.*, 1980; Yole and Irving, 1980). The western margin of North America is now thought to consist of a collage of terranes that have been transported to their present positions, commonly with a considerable northward component relative to the craton.

A persistent and important theme of the paleobiogeographic studies described below is the establishment of an autochthonous standard of reference with which the diversity and endemism of the displaced faunas can be compared. It is also important to keep the interval of time over which the analysis is made as narrow as possible because the position of biogeographic boundaries may fluctuate, causing a loss of resolution.

Permian fusulinid faunas deposited on (or in rocks physically linked to) the craton are divisible into a sequence of biotic provinces characterized both by their endemic taxa and a latitudinal diversity gradient (Monger and Ross, 1971; Yancey, 1975, 1979; Ross and Ross, 1981; Monger, 1984; Hallam, 1986). The Permian fusulinids of the allochthonous terranes can be divided into four categories (Figure 13): (1) terranes such as Quesnellia and Stikinia in British Columbia that show affinities to the autochthonous faunas of the southwestern United States and Mexico, a reflection of their northward displacement; (2) terranes such as the Cache Creek terrane which have affinities with the faunas of the Tethyan Ocean indicating considerable longitudinal displacement; (3) melange terranes such as the

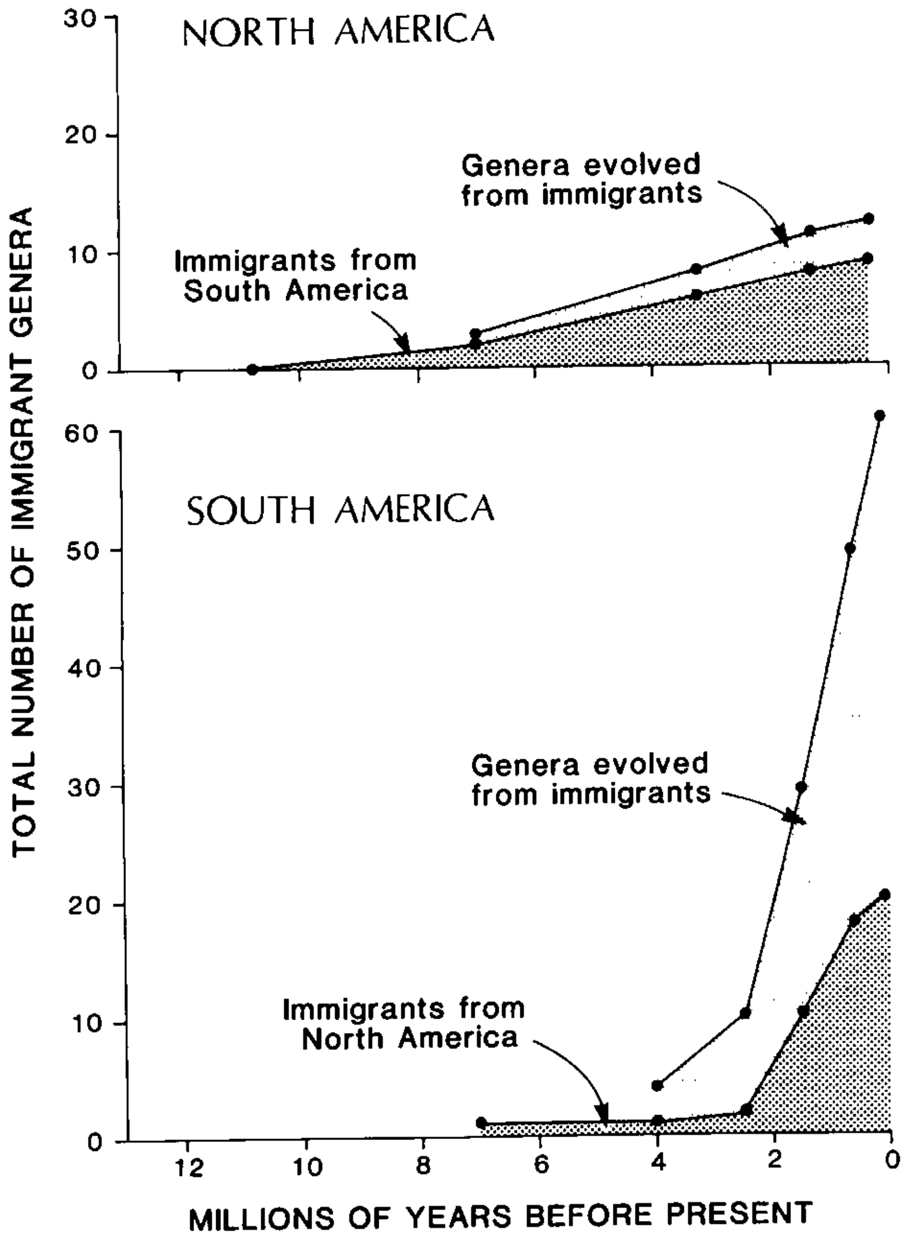


Figure 12 *The faunal dynamics of the Pliocene interchange between North and South America. Points plotted are mid-points of land mammal ages used in the paper of Marshall* et al. *(1982) from which the data originate.*

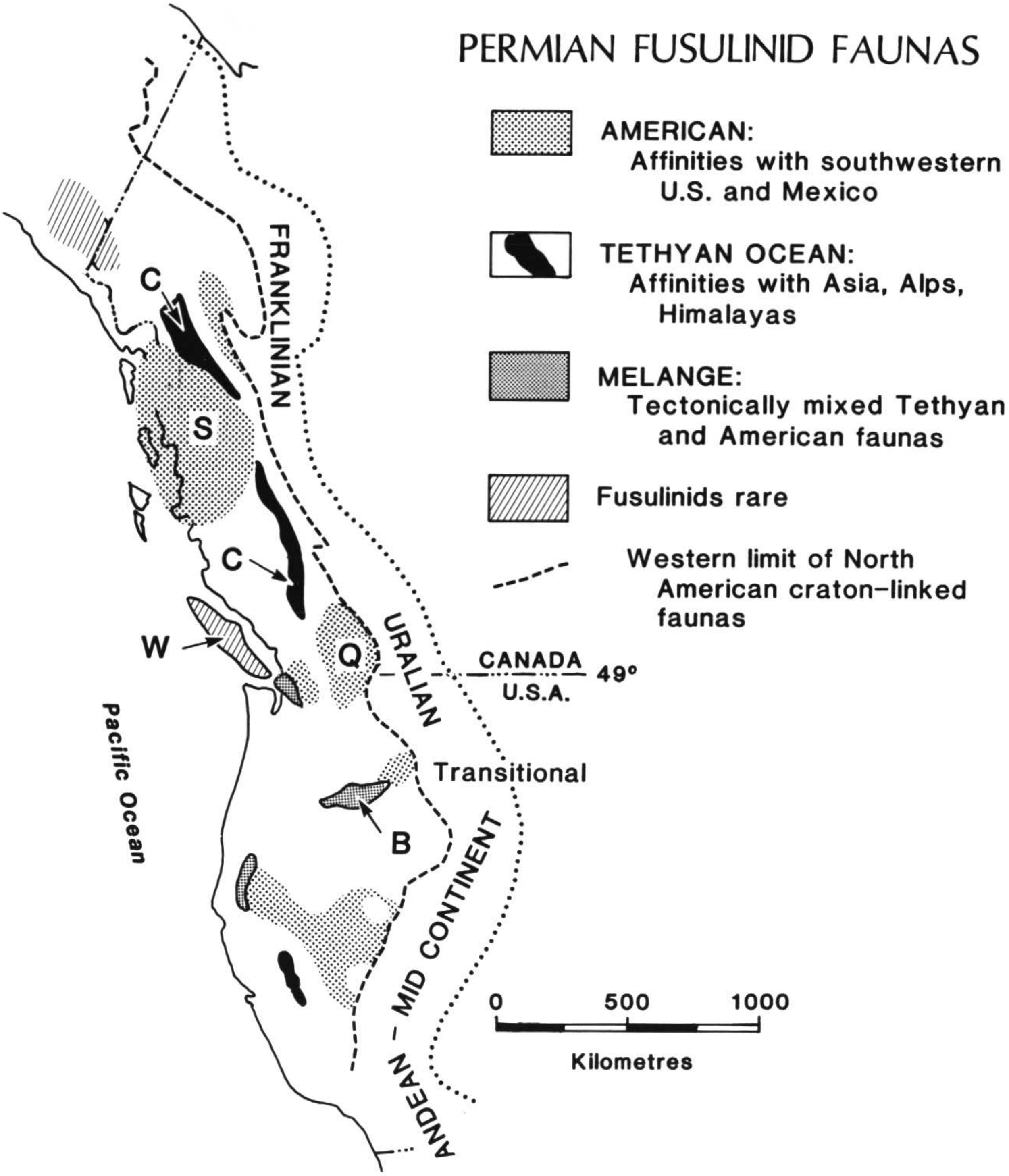
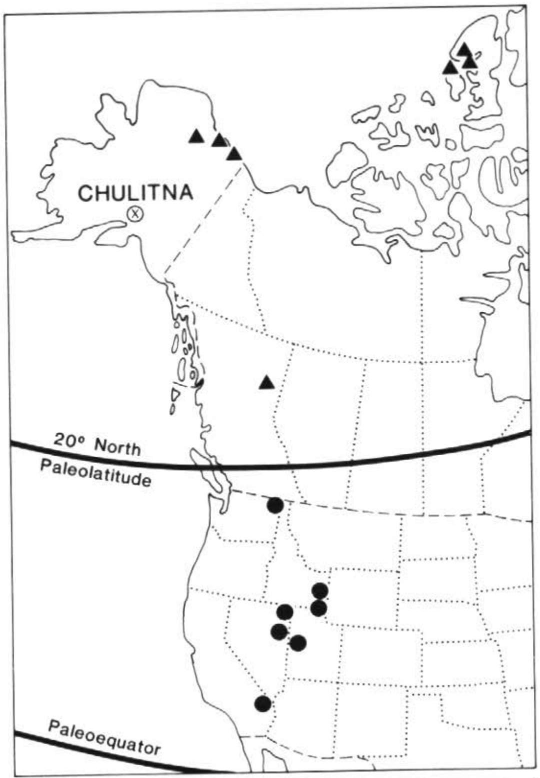
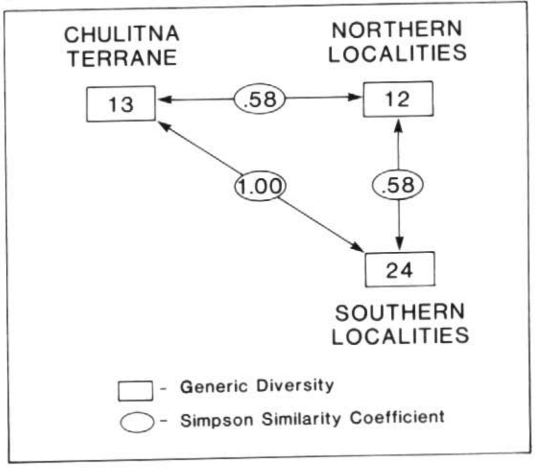


Figure 13 *Allochthonous Permian fusulinid faunas in the Cordillera (Monger, 1984). The Franklinian-Uralian and the Mid-continent-Andean faunas are on the craton. Allochthonous terranes referred to in the text are* **C**, *Cache Creek;* **S**, *Stikinia;* **W**, *Wrangellia;* **Q**, *Quesnellia;* **B**, *Baker.*

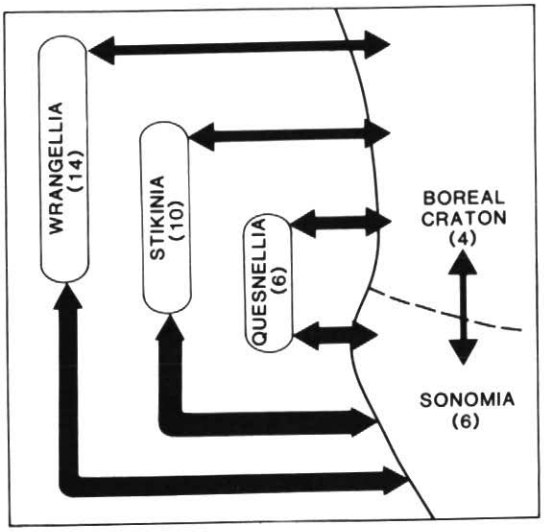
A


CHULITNA
20° North
Paleolatitude
Paleoequator

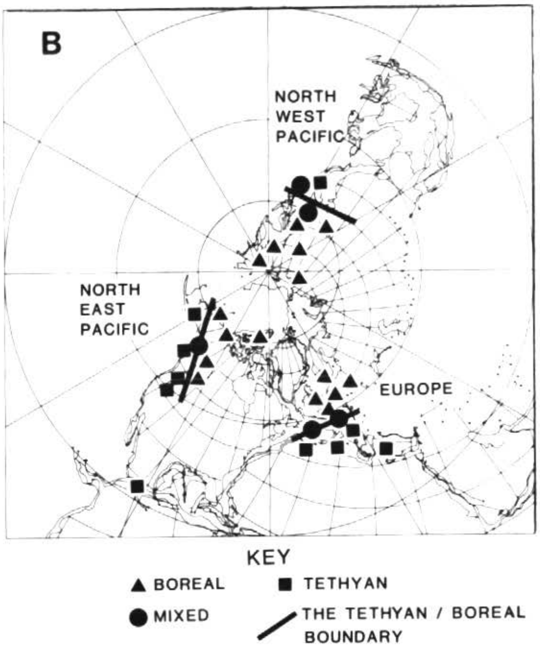
B


CHULITNA TERRANE
NORTHERN LOCALITIES
13
.58
12
1.00
.58
24
SOUTHERN LOCALITIES
- Generic Diversity
- Simpson Similarity Coefficient

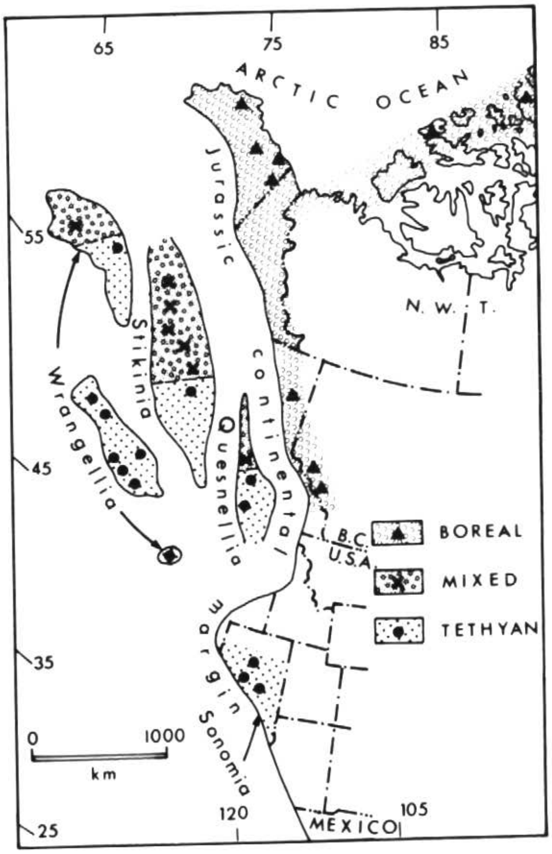
A


WRANGELLIA (14)
STIKINIA (10)
QUESNELLIA (6)
BOREAL CRATON (4)
SONOMIA (6)

A


B
NORTH WEST PACIFIC
NORTH EAST PACIFIC
EUROPE
KEY
▲ BOREAL
■ TETHYAN
● MIXED
THE TETHYAN / BOREAL BOUNDARY

B


65
75
85
ARCTIC OCEAN
Jurassic continental margin
55
45
35
25
Stikinia
Wrangellia
Quesnellia
N. W. T.
B.C.
U.S.A.
BOREAL
MIXED
TETHYAN
Sonomia
0
1000
km
120
105
MEXICO

Baker terrane in east-central Oregon in which fusulinid faunas of Tethyan and American affinities are tectonically mixed; (4) terranes such as Wrangellia with very few fusulinids but with common brachiopods and bryozoans which Monger (1984) suggests inhabited high (southern) paleolatitudes during the Permian.

Low, middle and high paleolatitude associations have been recognized for various Triassic stages of the North American craton (Tozer, 1982; Silberling, 1985). Scleractinian corals and megalodontid bivalves are present in the rich, low-paleolatitude faunas of Nevada with diversity declining northward. The Sverdrup Basin in the Arctic has yielded endemic ammonites and species of the bivalves *Posidonia* and *Monotis*. West of the craton margin, the low paleolatitude faunas occur as far north as southern Alaska. This pattern of disjunct diversity and endemism is well illustrated in a study of Chulitna terrane ammonites of the Smithian stage (Lower Triassic) conducted by Nichols and Silberling (1979). There are 20 genera in craton-bound Smithian rocks within 20 degrees north of the Triassic paleoequator. Rocks to the north of 20 degrees paleolatitude have yielded only 12 genera. A single limestone bed in the suspect Chulitna terrane of south-central Alaska has yielded 13 genera all of which are present in the southern faunas but only 7 of which are present in the northern faunas (Figure 14). At the species level the affinity with southern faunas is even more marked.

Biogeographic boundary off-set has been demonstrated by Taylor *et al.* (1984) and Smith and Tipper (1986) in a study of the Jurassic ammonoid biogeography of western North America. During the Pliensbachian, ammonites were separated into a northern circum-polar Boreal Realm and a southern Tethyan Realm. The area of overlap ran approximately parallel to paleolatitude in Europe and the northwest Pacific, but trended northwest-southeast in the northeast Pacific if the possibility of terrane displacement is not considered (Figure 15). The three Jurassic suspect terranes in western Canada are Quesnellia, Stikinia and Wrangellia. The two autochthonous, fixed reference areas with which the suspect terranes may be faunally compared are Sonomia (which accreted to the continent during the Triassic) and the cratonal faunas of the Fernie basin and the Arctic (Figure 16). The Canadian terranes show the strongest faunal similarity to Sonomia in keeping with the idea of post-Pliensbachian northward displacement, but there are mixed Tethyan/Boreal ammonite occurrences in the northern parts of the terranes. If the boundary is restored so that it parallels paleolatitude and reflects the pattern on the stable craton and elsewhere, it suggests a progressive increase in the amount of northward displacement of the Canadian terranes passing outboard from the continent with a latitudinal displacement for Wrangellia, for which the evidence is most convincing, of as much as 2,400 km relative to the craton. The patterns of ammonite diversity also support the concept of post-Pliensbachian northward displacement. Wrangellia sustained the most diverse ammonoid community, and diversity decreased progressively from Stikinia to Quesnellia to the craton (Figure 16A).

The genus *Amaltheus* is one of the components of the Pliensbachian Boreal fauna (Figure 15). Since it is northern and circumpolar in its distribution and since it occurs in the northern regions of all the Canadian allochthonous terranes, it demonstrates that the terranes must have been in the northern hemisphere during the Pliensbachian. This linking of a faunal distribution to one of the poles or "polar bear principle" as it has been called, is important because it can be used to resolve the north-south hemisphere ambiguity inherent in paleomagnetic data (Smith and Tipper, 1986). In addition, biogeographically linking suspect terranes to the cratonic plates flanking an ocean such as the Pacific can, in a general way, constrain the longitudinal position of the terranes. The Pliensbachian faunas of the North American suspect terranes, for example, have more in common with the craton-bound faunas of the eastern Pacific than those of the western Pacific.

As the Jurassic progressed, the North American plate moved northward and the molluscan Boreal-Tethyan transition occurred further south on the craton. By the Late Jurassic and earliest Cretaceous, the suspect terranes appear to have been within Boreal Realm and the biogeographic evidence becomes consistent with even zero latitudinal displacement relative to the craton (Taylor *et al.*, 1984; Jeletzky, 1984). However, on the basis of floristic provinces, Frederiksen (1987) recognizes significant latitudinal displacement of the latest Cretaceous rocks of Wrangellia, in keeping with paleomagnetic evidence of some 1600 km (Beck *et al.*, 1981) to 2400 km (Irving *et al.*, 1985) displacement of mid-Cretaceous granites on which the pollen-bearing rocks rest.

The Atlantic

Many of the interactions between the lithosphere and the biosphere tabulated in Figure 5 are illustrated by the Phanerozoic history of north European and North American faunas (Wilson, 1966). During the Cambrian and early Ordovician, a deep proto-Atlantic Ocean, called Iapetus, is thought to have separated the two regions. On one side, the faunas west of the Appalachians, of western Newfoundland, northwestern Ireland and Scotland were biogeographically coherent and contrasted markedly with the faunas of coastal New England, southern New Brunswick, Nova Scotia, eastern Newfoundland, England and northern Europe on the opposite shore (Cowie, 1971; Whittington and Hughes, 1973; Williams, 1973; McKerrow and Cocks, 1976). As the Iapetus Ocean closed, pelagic animals (graptoloids) filtered across the ocean first followed by animals with pelagic larval stages (brachiopods and trilobites) and then, in the Silurian, animals without pelagic larval stages (benthic ostracodes). Finally, freshwater fish crossed during the Devonian when there were non-marine connections between the plates. This period of faunal convergence and the tectonic suturing of fossilized endemic centres was followed by a re-opening of the Atlantic during the Mesozoic, as described above, and a time of faunal divergence between Europe and eastern North America as the Atlantic widened.

The pattern of faunal divergence caused by the opening of the Atlantic has been investigated by Fallaw (1979, 1983) using

Figure 14 ***(opposite page - upper left and middle left)*** *Disjunct diversity and endemism of the Smithian (Early Triassic) ammonite faunas of the Chulitna terrane. (Data from Nichols and Silberling, 1979)*

Figure 15 ***(opposite page - upper right and middle right)*** **(A)** *The Early Jurassic ammonite* Amaltheus *affectionately known as the braided lady because of its distinctive keel. This 3.5 cm diameter specimen is from southern Germany, but the genus is circum-polar in its distribution, occupying the Boreal region shown on the paleogeographic map* **(B)**. *Such distributions are useful for resolving the north-south hemisphere ambiguity of paleomagnetic data from displaced terranes. (Adapted from Smith and Tipper, 1986).*

Figure 16 ***(opposite page — lower left and lower right)*** *Early Jurassic ammonoid diversity and endemism and the displacement of terranes in western North America.* **(A)** *Plot of data for the Late Pliensbachian. Width of arrow shaft is proportional to the Dice similarity coefficient between the terranes indicated. Numbers are generic diversities for each terrane.* **(B)** *The north-south biogeograpnic zonation within the allochthonous terranes and on the craton. (Adapted from Smith and Tipper, 1986).*

distribution data for all marine fossils listed in the *Treatise on Invertebrate Paleontology* (Moore and Teichert, 1953-1973). He restricted the data to specific time intervals from the Jurassic to the Pleistocene and began by comparing faunas on either side of the Atlantic using the Simpson coefficient. The width of the Atlantic for the various time intervals was averaged from the distance between the 1000m isobath on eastern and western sides of the ocean measured from paleocontinental maps (Smith and Briden, 1977) at 10-degree latitude intervals. Figure 17A shows the negative trend of the correlation coefficient through time (as expressed by the ocean width) that characterizes faunal divergence. Fallaw went on to demonstrate an example of complimentarity by repeating the exercise for the Pacific Ocean and producing the positive correlation characteristic of faunal convergence (Figure 17B). Some geologists have long argued that the earth has been expanding (*e.g.*, Carey, 1976), but Fallaw's example of complimentarity does not support this hypothesis. As one ocean basin opened, another closed and endemism within the biosphere responded accordingly.

At the time of rifting and separation, a piece of the old European Plate (New England, New Brunswick, Nova Scotia and Newfoundland) was left tectonically sutured to the new North American Plate and a piece of the old North American Plate (Ireland and Scotland) was left sutured to Europe. The Early Paleozoic faunas of these plate fragments now form examples of disjunct endemism, anomalous paleobiogeographic patterns that were puzzled over long before the advent of plate tectonics.

Other Factors

This brief review has emphasized the potential direct connections between the history of the biosphere and lithosphere caused by changing plate configurations, but the rise, shift or demise of the various components of the plate tectonic model itself must have had considerable biogeographic impact. The island arcs of the Pacific, for example, are inhabited by most of the marine benthonic families in existence and the oceanic ridge system of the east Pacific plays host to a unique ecosystem based on sulphur-oxidizing bacteria rather than photosynthesis (Stanley, 1979; Flessa, 1980). The lithosphere can also influence the biosphere indirectly *via* the atmosphere and hydrosphere. It is obvious that changes in climate are experienced by plates as they migrate across the globe, but the configuration of the plates themselves may actually trigger significant changes in climate, particularly when a continent occupies a position over one of the poles. Stanley (1987) believes that plate tectonic-induced glacial episodes are one of the main agents of mass extinction.

Oscillations in sea level which radically influence biogeography may also be linked in part to plate tectonic processes. Rapid sea-floor spreading causes mid-oceanic ridges to displace the oceans onto the continental shelves (Hays and Pitman, 1973; Pitman, 1978). This, in turn, causes an amelioration of climate; an increase in the volume of epicontinental seas available for exploitation; a corresponding reduction in the area of the continents; and, if conditions are right, the connection of ocean basins by the formation of seaways across continental crust. Hallam (1981), for example, has argued that the formation of the Cretaceous seaway joining the Gulf of Mexico to the Canadian Arctic and dividing North America into two landmasses was one of the most important biogeographical events in the history of the northern hemisphere. It separated what Cox (1974) called Asiamerica (eastern Asia and western North America linked by a Bering land bridge) from Euramerica (Europe and eastern North America). The Turgai Sea running north-south across modern Eurasia separated Asiamerica from Euramerica on the other side of the globe. This is reflected in the distribution of plants and terrestrial animals as well as in the development of an endemic marine fauna within the American

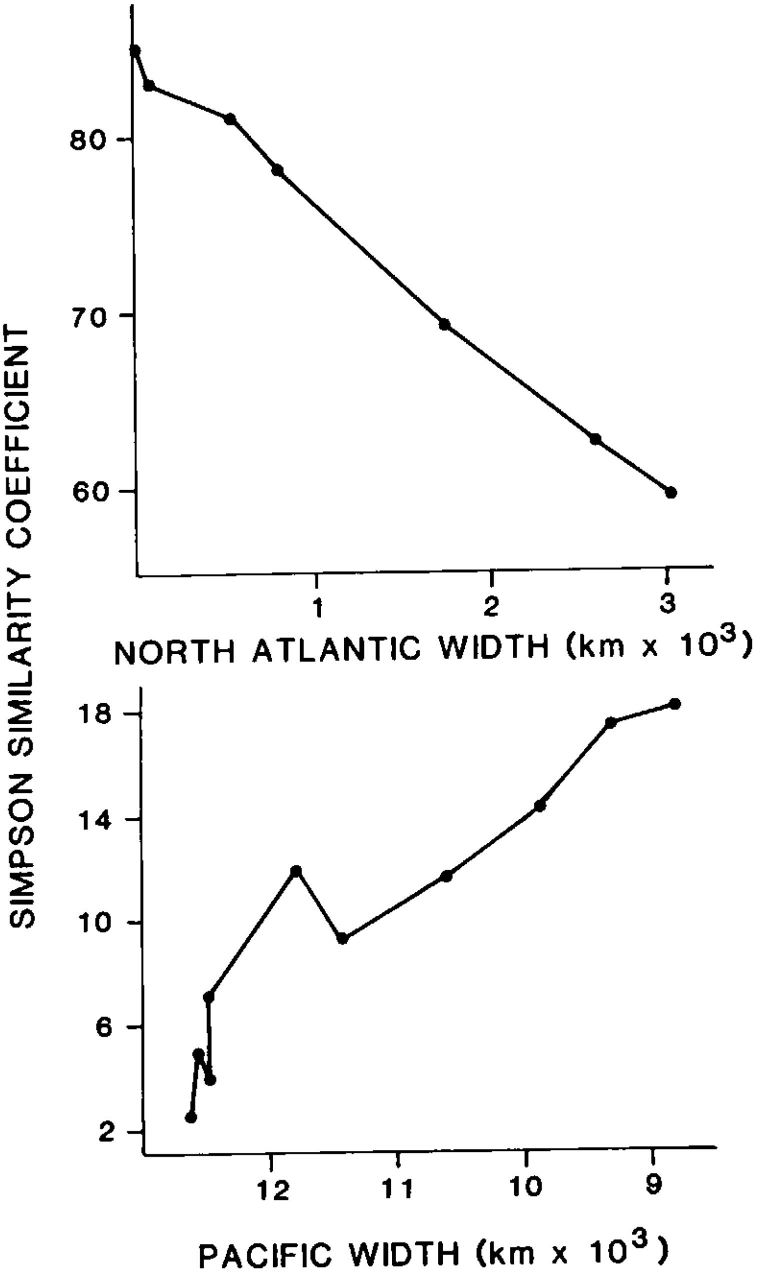


Figure 17 *Complimentarity: plate tectonic processes causing simultaneous faunal divergence and convergence. The correlation between ocean width and faunal similarity across* **(A)** *the Atlantic Ocean and* **(B)** *the Pacific Ocean since the Jurassic (Adapted from Fallaw, 1979, 1983).*

interior seaway itself which cut directly across paleolatitude. Among the better known endemic terrestrial animals are the tyrannosaurs which are restricted to Asiamerica and the iguanodonts restricted to Euramerica.

Conclusions

From the days of Wallace and Wegener to the modern problems of displaced terranes, paleobiogeographic anomalies have been the first to signal important underlying tectonic phenomena. However, the more comprehensive application of paleobiogeographic data to global tectonic problems and the reconstruction of paleogeography is subject to certain strengths and weaknesses. Collection and preservation failure cloud the picture, but at least the quality of collections can always be improved. Preservation failure can be alleviated to some extent by concentrating on well-skeletonized taxa that had a mode of life and inhabited environments that maximized their fossilization potential. Many species are inadequately defined, but if this problem becomes intractable, the paleobiogeographic picture can be considered at higher taxonomic levels.

Some important remaining questions for evolutionary biology concern details of the temporal patterns of convergence and divergence as the biosphere adjusted to new equilibrium states imposed by plate tectonics. From a geological perspective, reassembly of the jig-saw puzzle of disjunct patterns promises a continued contribution, particularly in terrane analysis. A positive feature of the predictive value of paleobiogeographic patterns is that they can be tested against internal and external criteria. Firstly, disjunct or temporal patterns displayed by one group of organisms can be checked against patterns seen in unrelated groups that occur in the same areas. Secondly, the concept of complimentarity predicts that in certain circumstances divergence in one sector of the biosphere will be accompanied by convergence in another. Finally, paleobiogeography may be tested against and, depending on the quality of the data, used to constrain, falsify or corroborate paleogeographic reconstructions based on geological and geophysical evidence.

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